

# Water and Food Acquisition and Their Consequences for Life History and Metabolism of North American Tortoises

Acquisition of sufficient food and water and the physiological consequences that occur when resource availability fluctuates are key to understanding the maintenance (Peterson 1996a, b), growth (Medica et al. 2012), reproduction (Henen 2002b), and health of tortoises (Jacobson et al. 1991) and wildlife populations generally (Robbins 1983). Diet information can inform studies on the nutritional requirements of herbivorous ectotherms (Nagy 1977, Christian et al. 1984, Bjorndal 1987, Pough 1973, Zimmerman and Tracy 1989, Troyer 1991, Oftedal et al. 2002, Tracy et al. 2006). Translating this information into nutritional status can be challenging, however, because of the tortoise's ability to persist for long periods without food or water and to amortize nutritional gains and losses over periods extending over years (Nagy and Medica 1986, Henen 1997, Peterson 1996b, Hellgren et al. 2000, Oftedal et al. 2002). In this chapter, we compare and contrast the acquisition of water, food, and their influence on nutrition in relation to tortoise life history and physiology.

Because of the paucity of information on smaller life stages of tortoises, the information here focuses on adults, unless specified. This distinction is important because of the challenges associated with the small body size of neonate and juvenile tortoises (hereafter called juveniles). Smaller body size has morphological, physiological, behavioral, and ecological consequences for juvenile tortoises relative to adults. For example, juvenile tortoises are smaller and weaker, cannot travel as far, and have reduced fields of view and relatively large requirements for body-building nutrients. Smaller tortoises also have body temperatures and hydric status that conform rapidly to ambient conditions; thus, internal stasis is challenging (Morafka 1994, Morafka et al. 2000). These factors tremendously influence requirements for drinking and accessibility to feeding opportunities that juvenile tortoises respond to by modifying their behaviors and increasing efficiencies.

Opportunities for water and food acquisition among North American tortoises are driven by environmental factors at

global, regional, and site-specific scales (chapter 9), as the five species' ranges nearly span the southern extent of the continent, encompassing the driest to wettest regions. For example, *Gopherus agassizii* near Barstow, California, experiences an average of ~104 mm of precipitation annually, while *G. polyphemus* in southwest Georgia experiences 1270 mm (Turner 1994, McRae et al. 1981). *Gopherus agassizii* experiences predominately winter rainfall, *G. morafkai* experiences 50:50 summer-to-winter rainfall in their north-central range (near Tucson, Arizona), and *G. flavomarginatus* experiences predominantly summer rainfall. *Gopherus berlandieri* has moisture availability that is intermediate between the three western-most species and *G. polyphemus*. The majority of rainfall for the eastern species occurs during summer months, enhanced by tropical storms, although the northern part of the range experiences relatively even amounts of precipitation throughout the year (Germano 1994). Precipitation variability is greater where the three western species live than for the other two species. Habitats spanning this range of conditions would seemingly result in divergent challenges for water and food acquisition. Closer inspection of the microenvironments that tortoises occupy reveals the similarities and differences in how tortoises acquire water and nutrition and in the strategies they employ to overcome environmental variability.

## WATER ACQUISITION

### Hydration

Tortoises require free water for hydration, and opportunities for water acquisition vary considerably among North American tortoises. *Gopherus agassizii* has the fewest drinking opportunities among North American tortoises. Extreme aridity (100–200 mm/y) and infrequent precipitation events demand that they drink whenever possible, including winter. Winter drinking for *G. agassizii* occurs at temperatures as low as 6°C (T. Esque and K. Nussear, unpublished data). It is striking to discover this ectotherm exiting hibernation

and actively drinking or wallowing below known hibernation temperatures of  $\sim 10^{\circ}\text{C}$  (Nussear et al. 2007). Activity at such low temperatures is a regular occurrence for the species in the northern part of its range, but is mostly unnecessary for the other species. In contrast to *G. agassizii*, *G. flavomarginatus* drinks primarily during summer storms (Adest et al. 1989, Brown 1994). Geographically intermediate to the other desert-inhabiting tortoises, *G. morafkai* receives winter and summer hydration as a result of the bimodal rainfall in the Sonoran Desert (Turner 1994, Turner and Brown 1994). Even though *G. morafkai* drinks in two seasons, the annual precipitation received in Tucson is within 10% of that in *G. flavomarginatus* habitat (NCDC 2012a, 2012b), and roughly twice that available for *G. agassizii*. *Gopherus berlandieri* also experiences bimodal rainfall patterns, with peaks in late spring and late summer (Hellgren et al. 2000). Drinking opportunities for *G. berlandieri* are intermediate between species to the east and west, but most similar to *G. polyphemus*, for which tropical summer storms dominate total precipitation and provide more than 40 mm of rain per month in the region (e.g., Tampa, Florida). In some *G. polyphemus* habitats, the water table is so shallow that there are drinking opportunities at the bottoms of their burrows (Ashton and Ashton 2008), at least seasonally. Furthermore, the high precipitation and abundant surface and subsurface water results in a mesic environment where evaporative losses are reduced overall. Because of the smaller body size and greater thermal reactivity, juvenile tortoises may have even more flexibility to respond to what would be considered seasonal drinking opportunities than adults. Juvenile *G. agassizii* are increasingly active in the mid- to late-winter season (late November onward, Wilson et al. 1999a) and, in the western Mojave Desert, this is the rainy season. Thus, juvenile *G. agassizii* adapt to challenges in water balance by shifting their activity to cooler periods, when the risk of water loss is decreased and water gain is increased. It is possible that the other juvenile tortoises respond in similar ways. The timing and amount of available rainfall governs drinking opportunities, which influence physiological demands in relation to other activities and triggers tortoises to respond as they can, sometimes in novel ways.

Drinking opportunities are also affected by variation in substrate materials, which influence surface flow, permeability, and infiltration, creating ephemeral catchments of water where tortoises drink. In western North America, areas of exposed bedrock moderate the availability of surface water after rains, depending on whether the parent material is relatively permeable (e.g., sandstone) or not (e.g., granite, basalt, or limestone). The two eastern tortoises occupy areas where sandy hammocks, limestone formations, river bottoms, and inundated wetlands have significant influences on the availability of resources for tortoises (Aufferberg and Franz 1982; chapter 9), such that drinking opportunities may be less available than expected in this mesic climate regime (Diemer 1986). Sandhill habitats are the driest areas within that region (Garner and Landers 1981), because coarse sand and gravel soils are well drained, and provide fewer opportunities for

drinking. In those areas, light rainfall percolates immediately as it falls and is largely unavailable as free water. In coastal areas, *G. berlandieri* occupies silt/clay-dominated lomas surrounded by bottomlands seasonally inundated by seawater. Further inland, the species occupies seasonally humid shrublands with sandy soils, where only heavy rains or patches of less permeable materials provide drinking sites (Rose and Judd 1982). Because of variable permeability among soil surfaces, intermittent puddling occurs in microsites that are patchy and widespread in the landscape.

Tortoises are not only opportunistic about drinking, but they employ active water acquisition, including environmental engineering and using their own bodies to form water catchments. *Gopherus agassizii* locates water catchments and revisits them as habitual drinking sites (Medica et al. 1980). This behavior is especially apparent on soils covered by desert pavement, a thin layer of interlocked gravel atop thin and semi-impermeable clay layers where the tortoises scrape gravel clear for drinking. *Gopherus agassizii* habitually uses dependable puddling locations and are known to gather in anticipation of precipitation on rocky outcrops, calcium carbonate hardpans, washes, and abandoned roadways (T. Esque, P. Medica, and K. Nussear personal observation). *Gopherus polyphemus* may drink in a manner that is no less novel by rising to their burrow entrances in response to rain, turning sideways, and extending their upslope forelimb to intercept the flow of water. Once individuals assume this position, the water pools on the apron of their burrows and they bend their heads over to drink from the pool (Ashton and Ashton 1991).

When rain pools or saturates soil surfaces, tortoises large and small drink by positioning their heads nearly perpendicular to the soil surface, pressing beak and nares toward the ground surface, and submerging their heads to the periocular region. Tortoises can also rehydrate from saturated soils by drawing moisture directly through their nares. This behavior is regularly observed among *G. agassizii* and *G. polyphemus*, and is undoubtedly important for other North American tortoises, especially those living in sandy areas (Ashton and Ashton 1991; chapter 9).

## Response to Drought Conditions

Drought has many technical definitions, but we define drought relative to environmental conditions: tortoise movement, body condition, physiology, and survivorship (Peterson 1996b, Duda et al. 1999, Longshore et al. 2003). Our definition of a severe drought is a one-year period with  $<50$  mm of precipitation. Climatic records indicate that these conditions occur fewer than 20 times over a 60-year period across the Mojave Desert and likely never in the ranges of the other tortoise species (NCDC 2012a, 2012b). Tortoises can respond to drought conditions by reducing energetic needs: for example, individuals of *G. agassizii* that were well hydrated and fed during a year of abundance (250% of normal winter precipitation) reduced their activity dramatically in a subsequent year with below-average precipitation (42 mm; Duda et al. 1999). During less intense dry periods, *G. agassizii* and

*G. berlandieri* both reduced movement and overall activity (Luckenbach 1982, Duda et al. 1999, Kazmaier et al. 2001c), presumably decreasing physiological demand. Dry conditions result in reduced activity and movement of most tortoises, making it even more difficult than usual to find individuals during surveys (R. Kazmaier, personal communication; Duda et al. 1999). Responses to drought conditions have not been published for *G. polyphemus*, but individuals may shift their activity areas toward more mesic sites during drought periods (Diemer 1986). It would be interesting to compare the results of water balance studies for the tortoises from more mesic environments during more stressful seasons or years with results on water balance in *G. agassizii* for comparative purposes.

### Water Balance and Physiology

Tortoises drink to replace water lost to dehydration from body surfaces and respiration (Minnich 1977). The vegetation that they eat contains excess salts and other compounds (e.g., sodium, chloride, and potassium; Peterson 1996b) that must be eliminated with urea from the body, resulting in water loss through excretion. Although tortoises are not thought to have evolved in desert conditions (Van Devender 2002b), they appear to be somewhat behaviorally and physiologically adapted to drastic changes in environmental conditions, making adult tortoises extremely resilient to osmotic fluctuations and water imbalance. To maintain water balance, tortoises decrease evaporation by altering their behavior, reducing activity, and retreating to burrows or caves with cooler, humid microenvironments until environmental conditions improve (Morafka 1982, Peterson 1996a, Nagy et al. 1997). These behaviors result in cutaneous water loss for *G. agassizii* (1.5 mg/cm<sup>2</sup> per day) that is less than a third of eastern box turtles' (*Terrapene carolina*) (5.3 mg/cm<sup>2</sup> per day; Schmidt-Nielsen and Bentley 1966). Although the majority of water loss by *G. agassizii* is through the integument and respiratory processes, both sources of loss are reduced relative to those of turtles in more mesic climates (Schmidt-Nielsen and Bentley 1966). Although juvenile tortoises employ all of the behaviors and physiology described for adults, their small size, and thus increased surface-to-volume ratios, increase hydration challenges considerably (Berry and Turner 1986, Hillard 1996, Wilson et al. 1999b). To reduce losses, juvenile tortoises shift activity periods. Because of their small size juvenile tortoises can opportunely become active much earlier than adults, often emerging in late winter (Naegele 1976, Diemer 1992a, Wilson et al. 1999a). Cooler activity periods means lower evaporative losses, and for *G. agassizii*, earlier activity coincides with the rainy season, thus increasing drinking opportunities and potentially feeding opportunities. Conversely, extended dry periods without summer precipitation put juvenile *G. agassizii* at risk of desiccation (Nagy et al. 1997), potentially explaining an important question about the species' demography: why are wild juvenile tortoises so rare? Perhaps the rigors of summer and generally dry conditions drive large losses of juvenile tortoises by desiccation in most years. Although winter behaviors and water balances have been explored, research on late spring and summer survivor-

ship through drought are difficult and costly to research and have not been fully explored.

During prolonged drought conditions, tortoises may lose up to 40% of their body weight, reducing their mean total body water volume by nearly 60% (Peterson 1996b). Drastic reductions in water volume in the bladder lead to increases in electrolyte concentrations in the remaining urine and increases in plasma osmolality (Nagy and Medica 1986). Reptiles use the urinary bladder, cloaca, and colon, rather than the kidney, to modify urine and plasma concentrations (Jorgensen 1998). The bladder plays a significant role in regulating blood osmolality, being highly permeable to water, urea, ammonia, and small ions, but not uric acid (Jorgensen 1998). This permeability allows tortoises in arid environments or those hibernating for weeks/months without fluid replacement to resorb water from the bladder and store highly concentrated wastes (e.g., uric acid), that can later be excreted quickly and completely when water becomes available for replacement.

Excreting excess salts (primarily potassium) requires balancing osmotic and ionic concentrations in urine and plasma using water or nitrogen. Excreting salts while conserving water requires removing nitrogen from the body that may be needed for other physiological processes (e.g., growth, reproduction). North American tortoises excrete waste mainly as uric acid or urates. One advantage of this process is that urates precipitate out of the solution in the bladder before fluids there are saturated. An active concentration process using water is therefore not needed, thereby avoiding water and energy losses. Tortoises must void the toxic bladder contents when opportunities arise and rehydrate, and tortoises can drink 11–28% of their total body mass (Minnich 1977, Nagy and Medica 1986, Peterson 1996b), simultaneously excreting materials ranging in consistency from syrupy tannin-colored water to granular grey wet-cement of a similar volume.

Because rainfall is tightly linked to food production for tortoises, periods exceeding one year with insufficient precipitation can cause declines in body condition (Peterson 1996b, Henen 1997, Nagy and Medica 1986), and periods longer than two years can result in high mortality for *G. agassizii* (Longshore et al. 2003). In retrospect, instances of drought-related mortality are widespread for desert-dwelling species: *G. agassizii* in Piute Valley, Nevada, in 1983 (P. Schneider, unpublished data); Goffs, California, in ~1996 (T. Shields, personal communications); and Ivanpah Valley, California (Peterson, 1994); and *G. morafkai* during the early 1980s in the Maricopa Mountains of central Arizona (82% decline; Wirt and Holm 1997). Given the dire consequences of prolonged dehydration in lands where seasonal dry periods are the rule, it is no surprise that tortoises do not pass up drinking opportunities when precipitation occurs, even if it interrupts hibernation.

### FOOD ACQUISITION

#### Foraging

Foraging behavior varies among tortoise species based on how environmental conditions interact with the plant spe-

cies available (fig. 10.1), and tortoise physiological condition. During years of low forage availability, *Gopherus berlandieri* and *G. agassizii* demonstrated greatly reduced activity (Kazmaier et al. 2001c; Ruby et al. 1994; Duda et al. 1999; USFWS, unpublished data). North American tortoises tend to be relatively quiescent from November through March, in response to relatively cool temperatures (Adest et al. 1989, Nussear et al. 2007, Van Devender 2002a, Diemer 1992a, McRae et al. 1981; fig. 10.1). Depending on environmental conditions in the previous year, springtime can be a period of nutritional need for tortoises, to recover from weight loss during winter, and to address nutritional requirements for females developing egg follicles and shells (Garner and Landers 1981; chapter 5). Two of the three western species demonstrate seasonally bimodal activity, with a spring feeding period, followed by decreased activity in the heat of midsummer, and resumption of activity with the advent of summer rains (Henen 2002, Van Devender et al. 2002, Adest et al. 1989, Kazmaier 2000, Birkhead et al. 2005). Too little information exists about the springtime activity of *G. flavomarginatus* for us to generalize. For *G. agassizii*, peak foraging occurs March through June (Woodbury and Hardy 1948, Burge and Bradley 1976, Esque 1994, Jennings 2002), and the diet consists of plants that thrive on winter rainfall. Occasionally, autumn feeding opportunities occur (Ofstedal 2002, Henen 2002a), resulting from localized summer rainfall germinating different annual flora than in the spring. Although *G. morafkai* feeds on spring annuals that are equally abundant as those in the Mojave Desert (Averill-Murray et al. 2002a), a broad survey of studies indicated that they feed primarily during summer and autumn (Van Devender et al. 2002; fig. 10.1). This pattern raises the question, why is *G. morafkai* not using the abundant spring vegetation that is available? Such a pattern is inconsistent with generalizations about tortoise opportunism in feeding and drinking. *Gopherus flavomarginatus* feeds from June through October (Morafka 1982), which is consistent with reliable precipitation and resulting food plants (Barbault and Halffter 1981; fig. 10.1). *Gopherus berlandieri* forages during late spring (April–May) and resumes feeding into the autumn (fig. 10.1). *Gopherus polyphemus* forages from April through September, coinciding with summer rainfall (fig. 10.1).

Tortoise foraging patterns are influenced by environmental conditions, habitat obstacles (e.g., topographic features and vegetation), cover site juxtaposition, and social interactions, but here we focus on variation in food availability. Most *G. agassizii* feeding occurs on sparsely vegetated, flat, or gently sloping outwash plains; however, some individuals forage on mountain slopes and boulder fields (chapter 9). Individuals meander during foraging bouts, frequently returning to their original cover sites, and sometimes making straight-line movements toward known cover sites (Esque 1994). *Gopherus agassizii* feeding has been described as nonrandom, because of repeated visits to the same feeding patches and because they follow washes (dry watercourses) in linear patterns, where “wash endemic” plant species are consumed (Jennings 1993). Tortoises also follow linear routes, along roadsides (P. Med-

ica, personal observation) and cultivated areas where food is abundant, and frequent well-used trails through vegetation (McRae et al. 1981). Individuals of *G. polyphemus* repeatedly return to their original burrows, but may have short-range seasonal migrations from mesic lowlands to drier highlands, driven by food competition in localized areas (McRae et al. 1981). Similarly, individuals of *G. flavomarginatus* use regular feeding routes with “rigid repetition” (Morafka 1982), and these routes may be travelled to take advantage of the fresh growth that results from previous foraging, similar to descriptions of foraging in the Green Sea Turtle (*Chelonia mydas*) (Bjorndal 1980). Alternatively, forays by *G. polyphemus* may be interspersed by longer meanderings into new areas where particular food species may be found (McRae et al. 1981, Ashton and Ashton 2008).

Foraging bouts for *G. agassizii* averaged 30 to 75 minutes in a day in the northeast Mojave Desert, and individuals spent 6–22% of their time foraging (Esque 1994). *Gopherus berlandieri* spent 6% of their active time feeding (Kazmaier et al. 2001c). For *G. berlandieri* and *G. polyphemus*, home range sizes were larger where food plants were scarce or widely scattered (Rose and Judd 1975; chapter 11), but McRae et al. (1981) cautioned against using home range size alone as an index of foraging investment because individuals may spend more time and travel farther while engaged in social interactions than feeding. *Gopherus agassizii* spent a smaller percentage of overall time feeding, with shorter feeding bouts, during years when food availability was low (Esque 1994). Individuals of *G. polyphemus* have a feeding radius within 30 m of their burrows (McRae et al. 1981), and *G. flavomarginatus* feeding travels have been described as like those of *G. polyphemus*, with males foraging over larger areas than females (Lieberman and Morafka 1988).

### Sustenance for Juveniles

Upon hatching or shortly thereafter (1–3 days), neonatal tortoises resorb the remaining egg yolk that is attached to intestines in a sac providing sustenance beyond the egg (Miller 1932)—a characteristic known as postparative lecithotrophy (Morafka et al. 2000). This process likely is crucial to survival in environments where feeding opportunities are unreliable for small tortoises. For example, emergent *G. agassizii* may find no feeding opportunities available on emergence from the egg, and such poor conditions frequently continue even into the spring activity season. As neonatal tortoises develop from lecithotrophy to herbivory, however, there is another crucial step in their ecology, requiring that they inoculate themselves with digestive symbiotic gut flora (Morafka et al. 2000). Inoculation may be accomplished by consuming soil or feces of adult tortoises containing the same symbionts (Troyer 1982).

Juvenile tortoises soon shift toward herbivory. It has been suggested that animal matter may play a significant role in nutrient acquisition, but few systematic studies have been conducted. Preference for insects over other diet items was demonstrated for *G. agassizii*, however, and consumption of animal matter has been noted for all North American tortoises (Okamoto 2002). Activity seasons for juveniles begin earlier in



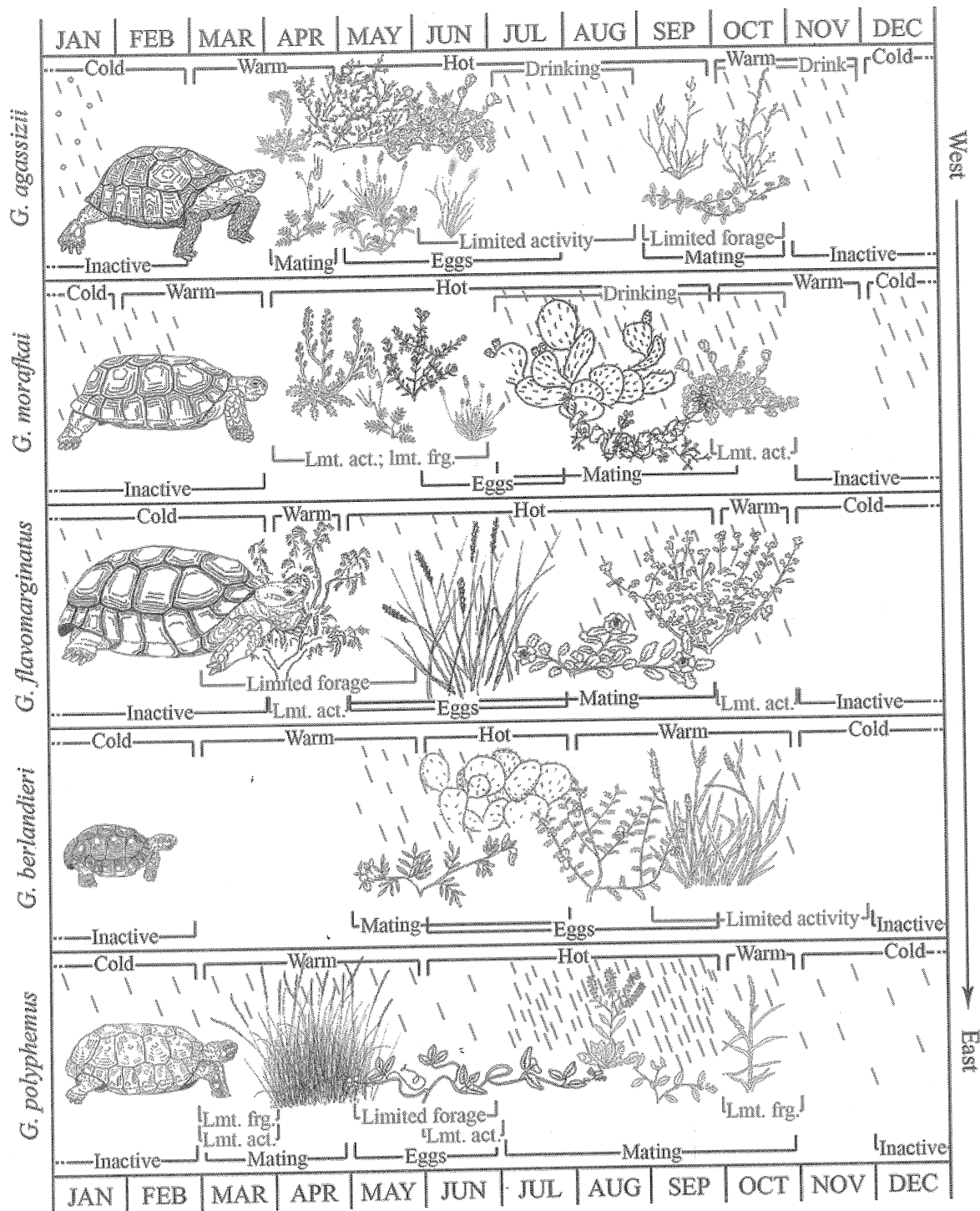


Fig. 10.1. Climate and timing of activity, foraging, and reproduction of North American tortoise species during the months of the year. Main precipitation periods are indicated with angled dashes (rain) and circles (snow). Foraging activity is indicated by the presence of plants specific to each species' diet. Sizes of tortoises are relative to each species' average MCL. Illustration by MA Walden, adapted from Morafka and Berry (2002).

the year than for adults. Interestingly, the activity shift means that some plants may be more accessible to the small tortoises with limited reach because during winter many herbaceous plants occur as basal rosettes that are easily in reach of the juveniles, prior to elongation (Morafka and Berry 2002). The

fresh young plants likely contain fewer structural materials and thus could also be more readily digestible than coarser mature plants.

While foraging, juveniles of *G. polyphemus* move constantly over relatively short distances ( $25 \text{ m} \pm 41.5 \text{ SE m}$ ), the time

outside their burrows is often brief ( $19.4 \pm \text{SE } 10.3$  min), and when disturbed they moved rapidly toward their burrows (Mushinsky et al. 2003, Halstead et al. 2007). Although the behaviors could provide protection from thermal extremes or have to do with feeding requirements or predator avoidance (Mushinsky et al. 2003), it was concluded that the “full stomach hypothesis” was the most likely driving factor, meaning that satiation took precedence over predator avoidance or temperature seeking behaviors (Halstead et al. 2007). Wild neonatal *G. flavomarginatus* spent 1% of their total time budget feeding, and “walk and feed” behaviors occupied 15 or 20% of their time in two different years (Tom 1988). During May and June, neonatal *G. flavomarginatus* foraged from 0900–1000 h, and during August through October they usually foraged from 1100 to 1200 h (Tom 1988). Seasonal consumption of dry food was estimated at 175 g dry matter for 2-year-old *G. agassizii*, and body mass increased by 34–55 g (Nagy et al. 1997).

Because their small body size translates into body temperatures that track ambient temperatures, small tortoises may increase feeding opportunities outside seasons when adults are normally active (Wilson et al. 1999a). Observations of juvenile *G. agassizii* during winter indicate that feeding was rare during October to January, but increased during warmer days beginning at the end of January (Wilson et al. 1999a). In contrast, adults in the area are not expected to be actively feeding until late March or April (Esque et al., unpublished data). Although temperature certainly plays an important role in activity periods, we suggest that foraging may also be linked to availability of plants that also only begin to elongate with warming winter trends and adequate rainfall. While research has focused on cool season activity in juvenile tortoises, there is little information available on warm season activities. We suggest that *G. agassizii* juveniles may behaviorally modify their body temperatures by avoiding extreme temperatures and the inherent cost of water loss that could be life threatening. Therefore, juveniles may shift their activity periods toward cooler season temperatures, thus increasing their overall activity seasons. No research on juvenile winter activity was available for the other North American species, however.

## Diet

Tortoise diet diversity is noteworthy. A compilation of reports throughout the range of *G. morafkai* yielded about 222 diet species (Van Devender et al. 2002) and, with sufficient observation, all tortoise species may prove to have similarly broad diets. *Gopherus agassizii* sampled about 50% (87 of 168 spp.) of the floras at each of two sites in the northeast Mojave Desert across five years. Three or four plant species comprised >70% of the diet at both sites in any year, however (Esque 1994, DeFalco 1995). In the western Mojave Desert, about 25% (44 of 173 spp.) of the flora at one site was sampled during a one-year study; ten species comprised >81% of the diet (Jennings 1993). Individuals switched diet species sequentially, following phenological patterns to acquire the freshest plants until only dry senescent plants were available (Jennings 2002). Individuals of *G. berlandieri* were observed foraging at one site for

several years and 29 plant species were included in tortoise diets (R. Kazmaier, unpublished data). In Florida, the diet of 50 *G. polyphemus* at one site consisted of 68 plant genera, including all common plant species in the area, but only ten species comprised 75% of the diet (Macdonald and Mushinsky 1988). In southwest Georgia, *G. polyphemus* consumed 53 genera, and individuals were considered opportunistic frugivores with fruit seeds—particularly of *Rubus* sp.—prevalent in spring and fall diets (Birkhead et al. 2005). Dietary analyses for *G. flavomarginatus* are not available, but observations indicate that they eat mostly tobosa grass (*Pleuraphis mutica*), supplemented by prickly pear cactus (*Opuntia* sp.) fruits and various herbaceous annuals (Morafka 1982). We speculate that their diets are most diverse when the summer annual flora peak.

Considerable speculation exists that juvenile tortoises consume qualitatively different diets than adults (Morafka and Berry 2002), and analyses of diets present mixed results. The few observations of juvenile *G. flavomarginatus* feeding identified mesquite (*Prosopis* sp.) flowers and green grass shoots, and tobosagrass (*Pleuraphis mutica*) was found in the feces of a juvenile (Morafka 1982). Diet selection was observed among juvenile *G. polyphemus*, including some species not abundant in adult diets (Mushinsky et al. 2003). During an El Niño year of increased precipitation, juvenile *G. agassizii* selected plant leaves (>70% diet) from the herbaceous annuals brown-eyed primrose (*Camissonia claviformis*) and desert dandelion (*Mala-cothrix glabrata*), while the annual Mediterranean grass (*Schismus* spp.) was avoided (Ofstedal et al. 2002). Selected plants were higher in water, protein, and PEP—an index of potential potassium excretion—but not lower in potassium than species that were bypassed (Ofstedal et al. 2002). Juvenile *G. agassizii* fed single-species diets lost phosphorus, shell mass, and volume on grass diets, regardless of whether the grasses were native or exotic (Hazard et al. 2010).

Dietary overlap generally is not widespread among North American tortoise species, except for the two desert tortoises. These two species have contiguous ranges, separated only by the Colorado River, and the plants do not differ greatly there. A synthesis of diet plants found 39 of 43 species occurred in both the Mojave and Sonoran Deserts, and nine species were diet items for both tortoise species (Ofstedal 2002). The wide latitudinal range of *G. morafkai* is sufficient to create mostly nonoverlapping diet lists between distal ends of the species' range, however. A similar pattern likely exists for *G. berlandieri*, but no data are available concerning its diet in Mexico. At least one native plant species (*Allionia incarnata*) is shared among the diets of the two desert tortoise species and *G. berlandieri*. Minimally, three species are shared between the diets of *G. berlandieri* and *G. polyphemus* (Macdonald and Mushinsky 1988; R. Kazmaier, unpublished data). *Gopherus flavomarginatus* also may have some dietary overlap with other species; however, data for a rigorous comparison are unavailable.

Food availability depends on the species richness, phenologies, and physical structures of plants, and the dietary preferences of the tortoises. Plant availability, palatability, and nutritional value differ among growth forms (annual forb,

Table 10.1. Percentages of diet eaten by North American tortoises within major plant growth forms

	Annual Forb	Annual or Perennial Grass	Perennial Forb	Woody Plant (vine, shrub, tree)	Succulent
<i>Gopherus agassizii</i>	52.9	12.6	19.5	11.5	3.4
<i>Gopherus morafkai</i>	*	30 to 53	7 to 28	6 to 22	**
<i>Gopherus berlandieri</i>	*	21.0	37.0	9.0	28.0
<i>Gopherus polyphemus</i>	20.0	7.0	46.0	20.0	**

Sources: *G. agassizii*: Esque 1994, DeFalco 1995; *G. morafkai*: citations in Van Devender 2002a; *G. berlandieri*: Scalise 2011; *G. polyphemus*: Macdonald and Mushinsky 1988.

\* Not eaten

\*\* Not determined

grass, perennial forb, woody shrub, tree, succulent) and plant parts (stems, leaves, flowers, fruits), partially because they differentially incorporate structural materials that can affect palatability and digestibility (McArthur et al. 1994). Fruits, on the other hand, may have particularly palatable parts that serve as attractants for animals, including tortoises, to encourage seed dispersal (Rick and Bowman 1961, Rose and Judd, 1982). Woody trees, vines, and shrubs play a role in tortoise diets when palatable parts such as twigs, leaves, flowers, and fruits are available (Van Devender et al. 2002). The presence of some woody plant parts in diets are difficult to explain. For example, pine needles and oak leaves ranked among the top five species present in the scats of *G. polyphemus* (Macdonald and Mushinsky 1988). It is hard to imagine that these plants provide nutritive sustenance—oaks have tannins that are difficult to digest, for instance—and the authors suggested alternative functions such as gut maintenance during hibernation. Perhaps these strange diet items fulfill an unknown function that will be revealed in the future.

Generally, perennial or annual forbs are the most important plant groups in diets of tortoises. Forbs are particularly important in *G. agassizii* diets, and moderately so for *G. morafkai* and *G. berlandieri* (Jennings 2002, Scalise 2011, Van Devender et al. 2002). Dietary differences between *G. agassizii* and *G. morafkai* may be related to the emergence of tortoises in the newly forming Mojave Desert from tortoises in the Sonoran Desert and their subsequent adaptation to conditions there (Van Devender 2002b). Forbs encompass the most diverse nutritional array and it is difficult to generalize about them; however, they have less structural fiber, which means that beneficial nutrients may be more accessible. Annual forbs and grasses are the most important items noted in *G. agassizii* diets (Woodbury and Hardy 1948, Hansen et al. 1976, Esque 1994, Oftedal 2002, Jennings 2002; table 10.1). Hohman and Ohmart (1980) found similar results, but with a seasonal shift to feeding on shrubs, from < 2% of diets in April to 20% in August. Surprisingly, although many *G. agassizii* diet species are available to *G. morafkai* (in some parts of their ranges), diets of the latter species are dominated by summer perennial forb species (Van Devender et al. 2002; table 10.1). Succulents (cacti) are particularly important components of the diet of *G. berlandieri* (Scalise 2011; Kazmaier, unpublished data; table

10.1). Perennial, rather than annual, forbs are dominant in the diet of *G. polyphemus*, but grasses are important in some areas (Macdonald and Mushinsky 1988, Douglas and Layne 1978). The range of observations demonstrates a great variability in the use of growth forms, but probably is influenced by presence or absence of various species and the other factors mentioned previously.

Questions about the benefit of grasses in the diets of North American tortoises stem from widespread invasion of annual and perennial exotic grasses, and consideration of their direct or indirect influence on tortoise health. Mediterranean annual grasses are fully integrated into western North American landscapes, and in the Mojave and Sonoran Deserts, and have the capacity to modify vegetation composition drastically. Although annual invasive grasses can have nutritional values similar to native grasses (Hazard et al. 2009, 2010), they can overwhelm ecosystems, reducing plant diversity and ultimately lowering overall nutritional availability. Invasive grasses also may affect tortoises directly: one study noted impactation of an invasive annual grass in tortoise mouths, for example (Medica and Eckert 2007). Jennings (2002) found few invasive grasses in the diet of *G. agassizii* during a one-year study. This finding apparently contrasts with findings from the northeast Mojave Desert, where invasive grasses were common in the tortoise's diet (Esque 1994): the principal forage species there included the several invasive grasses, such as brome grasses (*Bromus madritensis*, *B. tectorum*) and Mediterranean grass (*Schismus* spp.) (Hansen et al. 1976, Esque 1994). Jennings' (2002) observations were made during an extremely productive year, with a great diversity of nongrass plants available. In contrast to *G. agassizii*, *G. morafkai*, and *G. berlandieri* eat invasive (perennial) grasses, such as Lehmann lovegrass (*Eragrostis lehmanianna*) and buffelgrass (*Cenchrus ciliaris*), respectively (Morafka 1982; Kazmaier, unpublished data). Although the invasive perennial cogon grass (*Imperata cylindrical*) has very low nutritional value and is not eaten by *G. polyphemus*, it is a threat to habitat because it crowds native food plants and interferes with movement (Basiotis 2007).

Issues with invasive exotics aside, by most accounts grasses are important components in tortoise diets, and all North American tortoises eat substantial amounts of them. In addition, many African tortoises consume grasses as a large

portion of their diets (Kabigumila 2001). Grasses are important diet components probably because of their high relative abundances at certain times: they are less important when forbs are readily available (Garner and Landers 1981, Macdonald and Mushinsky 1988, Esque 1994, Scalise 2011). The low nutritional and high indigestible fiber content of grasses may account for lack of preference or avoidance by tortoises (McArthur et al. 1994, Ramirez et al. 2004, Basiotis 2007). *Gopherus polyphemus* eats early spring grasses, and switches to broadleaf grasses and legumes as they become available; then, in the fall, as forbs senesce, they switch back to grasses in some areas (Garner and Landers 1981). Overall, wiregrass (*Aristida beyrichiana*) was less favored than broad-leaved grasses (Garner and Landers 1981). Where choices are available, annual grasses are used to the near exclusion of perennial grasses, potentially because of their higher N, Total Nonstructural Carbohydrates (TNC), mineral content, and low fiber (Esque 1994; data in McArthur et al. 1994). One study found native perennial grasses to be absent from the diet of *G. agassizii* in April, but comprising approximately 10% later in the season (Hohman and Ohmart 1980). Others found *G. agassizii* eating dry grasses once well hydrated after summer rains (Nagy and Medica 1986). Native perennial grasses may be more important than currently documented in the diet of *G. agassizii*, and certainly comprise measurable portions of the diets of *G. morafkai*, *G. berlandieri*, and, sometimes, *G. polyphemus* (Van Devender et al. 2002, Scalise 2011). In general, tortoises may use grasses when more nutritious items are unavailable. Perhaps if the tortoises have slower passage times during these times—as predicted by digestive optimality (Tracy et al. 2006), they are able to obtain more nutrients than not eating at all, and over time gain mostly energy.

Prickly pear cactuses (*Opuntia* spp.) are the most widely available succulent plants to North American tortoises, and can be important for some species, especially when other plants are not available (table 10.1). The role of prickly pear cactuses in tortoise diets is interesting and not entirely understood at this time. They are considered to be survival food for *G. agassizii*, a seasonal benefit as a mast crop to *G. morafkai*, a staple in the diet of *G. berlandieri*, peripherally available to *G. polyphemus*, and possibly important in the diet of *G. flavomarginatus* (Morafka 1982). Although consumption of large amounts of prickly pear cactus over long periods of time is hypothesized to compromise tortoise physiology by potentially affecting calcium balance (Hellgren et al. 2000), prickly pear cactuses also ranked highest for mineral and carbohydrates content among 15 plant species analyzed for nutrition (McArthur et al. 1994). Beavertail cactus (*O. basilaris*) and pencil cholla (*O. ramosissima*) are used by *G. agassizii* during years when primary production is negligible (T. Shields, personal observation; T. Esque, personal observation; Turner et al. 1984). *Gopherus morafkai* also eats prickly pear cactus pads; and, in years of good fruit crops, the large fleshy fruits of Engelmann's prickly pear (*O. engelmannii*) are eaten with gusto. While the fruit is available, tortoises may have bright purple stains on their beaks and fore limbs. X-radiography

indicates that individuals may fill their entire guts with the fruits (T. Esque, personal observation). During times of low production, the diet of *G. berlandieri* also may be dominated by prickly pear cactus (Hellgren et al. 2000, Kazmaier 2000), including Texas prickly pear (*O. lindheimeri*) and desert Christmas cactus (*O. leptocaulus*), both of which are especially important components of the summer diet (Auffenberg and Weaver 1969, Scalise 2011). Both *G. flavomarginatus* and *G. polyphemus* also eat prickly pear cactus (Morafka 1982, Macdonald and Mushinsky 1988, respectively).

All young, growing animals have energy and nutrition requirements that surpass those of adults (adjusted for size), because of their need to synthesize growing bodies (Nagy et al. 1997, Morafka et al. 2000). Efficient foraging, by gathering high quality food items, can be essential to juvenile tortoises, because high quality diets result in faster growth, and increased size reduces predation risk. Faster growth also is commensurate with more rapid attainment of sexual maturity (e.g., in *G. polyphemus*; Halstead et al. 2007; chapter 7). Although some growing animals increase their metabolisms to accommodate growth needs, juvenile tortoises do not. Therefore, they must make up nutritional demands modifying behaviors to be more efficient, and there is speculation that they choose richer diets, although it has been noted in one experiment that nutritional quality of *G. agassizii* juvenile diet does not differ from that of adults. Other ways of increasing nutritional content include eating higher quality or more digestible plant parts. A demonstration of such preferences includes strong avoidance of wiregrass by juvenile *G. polyphemus*. Wiregrass has relatively low nutrition value compared to other forbs and some grasses (Mushinsky et al. 2003).

### Nutrition and Metabolism

Tortoise nutrition is the sum of energy, protein and amino acids, minerals, vitamins, water, and other components of plants used as the building blocks for healthy tortoises. The majority of energy tortoises receive comes from carbohydrates and through fermentation of the fiber in the plants they eat (Bjorndal 1987). The time and distance tortoises forage is a function of forage availability, but as their guts become full, some digestion is required to make room for additional food prior to consumption. Food passage rates are temperature dependent (Bjorndal 1987, Troyer 1991, Dean-Bradley 1995, Zimmerman and Tracy 1989); thus, foraging behavior is intimately related to tortoise physiology and thermal biology. Tortoises also supplement their diets with nonvegetative materials such as animal matter for protein and supplemental mineral nutrition. Nutrition analyses of tortoise food plants indicate some important correlations. One study of plant nutrition found that although nutritive and mineral content of food plants varied between two soil types (i.e., sand versus carbonate parent materials), the availability of precipitation had a larger influence on plant nutrition than variation in soil parameters (McArthur et al. 1994). Generally, plant species that are high in protein and low in fiber are also high in energy content, calcium (Ca), magnesium (Mg), phosphorus (P), and

potassium (K) (Tracy et al. 2006). Another study found that plants with higher water content were generally correlated with better nutritive and mineral content, and high protein was correlated with high fat content; protein was negatively correlated with Acid Detergent Fiber (ADF—primarily compounds for structural materials), and TNC and Acid Detergent Fiber were negatively correlated (McArthur et al. 1994).

In chelonians, the thyroid gland plays a central role in regulating metabolism and maintaining physiological balance. The structure of the thyroid gland and the hormones it produces are very similar across vertebrate taxa, and the hormones have a wide variety of functions. In reptiles, thyroid hormones such as tri-iodothyronine (T<sub>3</sub>) and tetra-iodothyronine (T<sub>4</sub> or thyroxine) play an integral part in growth and development (Maher 1961, 1965), regulation of nutrient assimilation (Eales 1979, Kohel et al. 2001), reproduction (McNabb 1992), ecdysis (Lynn 1970), behavior (Steinberg et al. 1993), and metabolism (Maher 1961, 1965). Thyroid hormones bind to mitochondria and activate enzymes involved in glycolysis and ATP production, which increases the rates metabolism in target tissues. These hormones also influence a wide variety of peripheral tissues, by elevating oxygen and energy consumption and increasing heart rate, blood pressure, and sensitivity to sympathetic stimulation. Although thyroid functions are diverse, their primary role is to support energy-demanding activities that occur when environmental conditions are favorable (Eales 1979). A comparison of thyroid functioning in reptiles and mammals concluded that although the reptilian thyroid is active at high temperatures it is still considerably less active than the mammalian thyroid (Hulbert and Williams 1988). Desert tortoises were at the lower end of the range reported for thyroxine levels compared to other reptiles, indicating a very low metabolic rate.

Thyroid activity in North American tortoises is most important in metabolism and is positively influenced by temperature and seasonality (Kohel et al. 2001). For tortoises in temperate climates, we would expect thyroid hormone production to increase during seasons with increased metabolic activity, such as feeding, growth, and reproduction or surface activity, and decrease during periods of metabolic quiescence, such as hibernation (McNabb 1992, Gerwien and John-Alder 1992, Kohel et al. 2001). Studies examining the effects of plasma thyroxine (T<sub>4</sub>) levels in *G. agassizii* (Kohel et al. 2001) and the Painted Turtle (*Chrysemys picta*) (Licht et al. 1985) described distinct monthly and seasonal changes in thyroxine levels, as well as differences related to sex, size, and reproductive activity. Thyroxine levels were lowest during hibernation and increased during spring emergence, when tortoises increase feeding and activity, all of which have been implicated with activation of the hypothalamo-pituitary-thyroid (HPT) axis (Kohel et al. 2001). Thyroxine levels also are influenced by nutrient uptake. For example, individuals of *G. agassizii* that were fasted for a two-week period had decreased thyroxine levels (Kohel et al. 2001), but those levels increased within 36 hours after feeding, suggesting that nutrients activate the HPT axis (Eales 1988, MacKenzie et al. 1998). The thyroid response

to food intake may be an important factor in stimulating increased metabolic activity for tortoises as they emerge from winter hibernation, supporting increased metabolic needs after emergence.

### Nonvegetation Food Items

The diversity of diets appears to be driven in part, by sampling potential foods and accidentally ingesting materials that occur near target food items (Van Devender et al. 2002), and tortoises occasionally ingest manufactured objects such as human trash (Macdonald and Mushinsky 1988, Walde et al. 2007). Feeding observations have also documented tortoises consuming the feces of congeners and other animals (Auffenberg and Weaver 1969, Garner and Landers 1981, Esque and Peters 2004, Walde et al. 2006). Observers are fascinated when tortoises ingest nonplant items, yet this behavior is widespread and possibly has a nutritional basis. Tortoises have widely been observed ingesting: soil at mineral licks, a variety of bones, snail shells, raptor pellets, charcoal, sand, and stones (Auffenberg and Weaver 1969; Sokal 1971; Hohman and Ohmart 1980; Marlow and Tollestrup 1982; Macdonald and Mushinsky 1988; Esque and Peters 1994; Murray 1997; Hellgren et al. 2000; Stitt and Davis 2003; Walde et al. 2007; Kazmaier, unpublished data 2012). Individuals of *Gopherus polyphemus* have been observed carrying bones to their burrows and eating carrion (Garner and Landers 1981). Insect matter was the fourth-most abundant material in *G. polyphemus* scats (Macdonald and Mushinsky 1988). Selection of animal matter by *G. polyphemus* may be motivated by low phosphorus, calcium, and protein concentrations in its food (Carr 1952), all of which are needed for egg formation (Garner and Landers 1981). Growing tortoises require minerals and female tortoises require additional mineral expenditures for eggshells. It has been hypothesized that female tortoises mobilize CaCO<sub>3</sub> from their own bones during eggshell formation, but also supplement dietary calcium when possible (Hellgren et al. 2000). Alternative hypotheses include nonfood items as geoliths for food mastication and vermifuge for the removal of internal parasites (Marlow and Tollestrup 1982, Macdonald and Mushinsky 1988, Esque and Peters 1994). Although intriguing the overall importance of animal matter in tortoise diets remains physiologically unexplained.

### NUTRITIONAL ECOLOGY: DIET SELECTION

Diet selection is the preferential use of foods by individuals or populations and is usually quantified by the relative use of a food item with respect to its availability. Preferred plants are those eaten in greater abundance than if tortoises found them at random, while avoided species are eaten less frequently than their availability in the environment would indicate. Food items that are neither preferred nor avoided appear to be used randomly. Does diet selection occur for specific plant species or qualities of plants? If diet selection occurs, what are the common dietary characteristics of the plants that are selected (e.g., energy, minerals, vitamins, or



water)? Diet selection analyses have documented preferences for the *Gopherus polyphemus* (Macdonald and Mushinsky 1988), *G. berlandieri* (Scalise 2011), and *G. agassizii* (Esque 1994, Jennings 2002, Tracy et al. 2006). Some items, although widely available and frequently investigated by these species, were never observed in diets; while other species that were rare in the environment were disproportionately represented in diets or were not quantified during vegetation surveys, even though they were consumed (Macdonald and Mushinsky 1988, Esque 1994, Jennings 1993). Although grasses are important diet components across species, it is probably because of their high relative abundances at certain times: they are less important when forbs are readily available and are consumed at the frequency with which they occur in the environment (eaten at random), and generally are avoided (Garner and Landers 1981, Macdonald and Mushinsky 1988, Esque 1994, Scalise 2011). The most frequently ingested food items (grasses) for *G. polyphemus* were eaten at random with respect to their abundance in the environment, but one highly preferred genus (*Richardia*) was among the most nutritional diet plants (i.e., high in water, fat, Ca, and other mineral content) (Macdonald and Mushinsky 1988). Diet and preference data pooled among five sites throughout the range of *G. berlandieri* within Texas indicated that it prefers cactus, avoids grasses, and eats forbs and woody plants at random (Scalise 2011). *Gopherus agassizii* also demonstrated preferences (Esque 1994, Tracy et al. 2006), but in contrast to the other two species. Diet selection was found to vary by the plants' phenological state, with fresh plants preferred and dried plants avoided until nothing else was left (Jennings 2002). No single species was consistently preferred or avoided among years in the northeast Mojave (Esque 1994). Both native and invasive species were among the preferred plants, and the patterns varied among years in relation to the number of species available.

Tortoise diet selection data can be used to support or refute theories about diet and foraging optimality (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Stephens and Krebs 1986), nutritional wisdom (Westoby 1974), and functional response (Spalinger and Hobbs 1992). Diet selection data can be coupled with experimentation on nutrition and digestive efficiency to explain the relative amounts of nutrients in tortoise diets and what they contribute to tortoise health. Ultimately, such work can be placed in the theoretical context of physiological ecology to explain animal nutrition (Tracy et al. 2006). Attempts to describe observed diet and nutrition patterns mechanistically include many theoretical contexts: digestive efficiency costs (Nagy and Medica 1986); energy assimilation (Bjorndal 1987); self-selection (Waldbauer and Friedman 1991); and the cost of switching food types (Tracy et al. 2006), all reviewed in relation to North American tortoises by Oftedal (2002) and Tracy et al. (2006). In this framework, Oftedal et al. (2002) and Tracy et al. (2006) integrated scientific theory, field observations, and laboratory experiments to generate alternative hypotheses for understanding tortoise nutritional ecology, specifically for *G. agassizii*. The Potassium Excretion Potential (PEP) Index hypothesis hinges

on the need for tortoises to excrete excess K in the form of urates, resulting in a high ratio of water and nitrogen to potassium and requiring large amounts of nitrogen and water (Oftedal 2002). According to this hypothesis, tortoises lose so much nitrogen and water in the process of eliminating excess K that they must select plant species of high PEP Index to avoid nutritional deficits. Observations of growing tortoises in semiwild conditions and feeding on freely available plant species, indicated that they selected plants with a high PEP Index from among all the plants available, supporting the PEP Index hypothesis, although K was not avoided specifically. It is widely observed that several plants with high PEP values are eaten vigorously by tortoises when they are located, but that many of these plants such as locoweeds (*Astragalus* spp.) or evening primroses (*Oenothera* and *Camissonia* spp.) are usually uncommon; thus, they likely do not make up large portions of diets in most years. In contrast, Tracy et al. (2006) found that *G. agassizii* neither avoided plants with high K nor preferred plants with high PEP indices. They noted that the diets of individuals did comprise a subset of available plants, and that the preferred species were those that remained green for long periods of time: tortoises consumed these species until "switching" was necessary (Tracy et al. 2006). Based on these results, Tracy et al. (2006) developed the Integrated Resource Acquisition Hypothesis (IRAH) by integrating aspects of optimal foraging, optimal digestion, and cost-of-switching hypotheses. In the IRAH, nutritional value is increased by feeding on a few plant species that the tortoise finds readily available and that the symbiotic gut flora are already used to (i.e., switching would require adjustments of the gut flora, leading to inefficiencies in digestion), and feeds on them until they are unavailable, then switches to another green species, until finally feeding on cured materials. Interestingly, this is the pattern of foraging that was also described for an independent site in the northwest Mojave Desert (Jennings 2002). This exciting and relevant field of work demands future synthesis including other species of tortoises.

## CONCLUSIONS

Although the availability of drinking water varies considerably among North American tortoises, acquisition of free-standing water is essential for tortoise survival. The basic physiological hardware to respond to this variability is similar among tortoises, but behavioral responses are surprisingly variable among species and between adults and juveniles. Arid conditions appear to be most challenging for juvenile tortoises, yet few systematic studies quantify juvenile performance during the most arid seasons. The diets of North American tortoises include a broad sample of all plant species available in their habitats, but a small subset of plant species usually comprise the majority of diets. Nutrition may be supplemented with minerals and protein from animal matter and juveniles may particularly benefit from nonvegetative diet items, but most of such observations are anecdotal and more work on this aspect of tortoise nutrition is warranted. Although grasses



and cactus are widely prevalent among adult tortoise diets, grass-dominated diets may be nutritionally detrimental to juvenile tortoises and may have important consequences for tortoise populations in habitats where invasive grasses dominate plant communities. There is debate in the scientific community regarding the mechanistic underpinnings of tortoise foraging, diet, and nutrition. Additional research in this field would benefit the conservation and management of North American tortoises.

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